

Criteria for the Indication of Center of Origin in Plant Geographical Studies*

STANLEY A. CAIN

When the flora or fauna of any region is considered taxonomically or geographically, it becomes apparent that it bears relationships with surrounding regions. The taxonomist, phylogeneticist (if he be different from a taxonomist), and the geographer are inevitably confronted by problems of origin and migration.

Forty years ago Charles C. Adams published a pioneer series of papers on postglacial dispersal of biota in North America (Adams, 1902a, 1902b, 1905, etc.), outstanding in their conception of process in biogeography. In one of these papers Adams (1902a) listed 10 criteria for the determination of centers of origin, and they were later reiterated (Adams, 1909) with further comments. Insofar as I know, these criteria have never been critically analyzed, although the concept of center of origin has been attacked by Kinsey (1936). Rather, they have been largely accepted without question, despite the lack of substantiating data in some cases, and have been variously and somewhat loosely employed. It is time for an appraisal: thus it is the purpose of this paper to review these criteria in the light of more recent contributions to the science of plant geography. Findings in the field of genetics, in particular, and in the study of wild populations supply reasons why certain of the criteria can not be tacitly accepted.

The concept of center itself should be broken down into its various implications. (1) *Center of origin* refers only to the region in which a population or a phyletic stock had its origin in an evolutionary sense. (2) *Center of dispersal* coincides with the center of origin only for the original members of a group. (3) *Center of variation* is the region where there is the largest number of biotypes within a species, species within a section, etc. (4) *Center of frequency* refers to the area with the densest population of the kind or kinds under consideration. (5) *Center of preservation* is an area where, usually, several species of a flora have survived a generally unfavorable change of environment. These are the epibiotic or relic members of the flora of a region. The differences among these centers are not always apparent in the literature.

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This paper has been shortened due to the space limitations of the Journal. A fuller treatment of these problems may be sought in the author's "Foundations of Plant Geography," to be published by Harper and Brothers.

The literature of plant and animal geography, taxonomy, and evolution is replete with statements concerning the center of origin of certain species, species groups, genera, etc. For example, Babcock and Stebbins (1937) say, "The distribution of the genus *Youngia* taken as a whole is entirely consistent with the conception that it is a natural group which had its origin in southeastern Asia and that evolution has been accompanied by extension of the geographic range." On the other hand, some species, as recognized by taxonomists, may not have had a center of origin in the sense of a restricted geographic spot where they arose. For example, Gleason (1923) states:

" . . . Probably if a complete series of specimens were at hand, showing comprehensively the maples of the eastern states, for example, from the Pliocene to the present time, it would be seen that some of the earlier forms are absolutely continuous with our present species and that the slight morphological distinctions between them are only the result of continuous slow variations throughout the centuries. According to this view, many modern species had no localized origin and are not the off shoot of any parent, but represent the mass development of a species, which, under our present taxonomic ideas, came to a stop at the beginning of a break in our geological record of it and reappeared as a new species at the beginning of our next experience with it."

A different situation is emphasized by Kinsey (1936), who denies both the usefulness and the truth of the concept of center of origin. He demonstrates through his taxonomic work with the gall wasps that species differ by many genic factors that have been added gradually to the population as it has migrated. Some of the characters of a species have been added in one place, and others in other places, and certain gene frequencies have increased with isolation resulting from migration. Where, then, is the center of origin? I think it would be begging the question to say that the center of origin of a species is where the genic factor or factors causing reproductive isolation arose.

Two other situations can be mentioned in which, in the strictest sense, there is no single center of origin. Chromosome (genom) doubling may happen many times in many places in a diploid population. The resulting autotetraploids, which may be a good species, do not necessarily have a center of origin other than the area of the entire progenitor diploid population. The map of Baldwin (1941) showing the chromosome races at *Galax aphylla* is of interest in this connection. Also, it is becoming increasingly apparent that many plant species are of hybrid origin. Sometimes a swarm of diploid hybrids, segregates, and backcrosses have attained a sufficiently distinct character and area that their population has been given specific status, distinct from the original species. At other times polyploid complexes develop. Stebbins (1940) says, "Dissolution of genetic barriers and exchange of genes between genetic systems that are completely isolated from each other in the diploid condition are made possible by the synthesis of polyploid complexes through allopolyploidy between three,

four or more species, following the introduction of genes from all the species concerned." (See also Babcock and Cameron, 1934; Goodspeed and Bradley, 1942.) For example, according to the studies of Camp (1942), *Vaccinium corymbosum* is a tetraploid hybrid complex that has no center of origin in the usual sense. One contributing tetraploid was originally Ozarkian (*V. arkan-sanum*), one was in the Appalachian upland (*V. simulatum*), and one was of the eastern coastal plain (*V. australe*).

With these qualifications concerning types of centers and with the realization that under certain circumstances there may not be a center of origin, there follows a consideration of the criteria proposed four decades ago by Adams.¹

CRITERION 1. LOCATION OF GREATEST DIFFERENTIATION OF A TYPE

With reference to this criterion of center of origin, Adams (1902a) says, "It is a very fundamental law that most forms of life are confined to restricted areas and only a small number have extensive distribution. Thus, from the center of origin there is a constant decrease, or attenuation in the number of forms which have been able to depart far from the original home."

This criterion is legitimate and applicable if we make two assumptions. In the first place, the basic assumption underlying the whole thesis is that there is a center of origin for a phyletic stock. This has already been discussed in the introduction. The other assumption is that there is a time relationship in evolution, that polymorphism increases with time; and that there is an age-and-area relationship, that with age the population of a species or other group tends to increase and occupy a wider area. In this connection see Willis (1922, 1940) and the numerous expert criticisms of his hypothesis. If we can accept these assumptions, it is clear that there will tend to be more polymorphism in the region of origin of a phyletic stock than away from this center. In such a region there will be more forms (biotypes, subspecies, species, sections, etc.) because of the longer time in which evolution has been occurring in the steadily increasing numbers of different kinds. With time, some of the forms originating in the central region will attain wider areas. They, in turn, may give rise to new forms away from the center, but in the nature of the relationship, the original area will tend to exceed any derived peripheral area in the number of kinds represented.

¹ I wish it understood that the evaluation of them is in no way a specific attack on Adams' paper, which was breaking new ground at that time, but is rather a criticism of the present day employment of these rules without evaluation of them in the light of more modern knowledge, and recognition of their limitations. As a matter of fact, by 1909 Adams was careful to point out that he understood the criteria to be only "convenient classes of evidence to which we may turn . . . It should be clearly emphasized that it is the convergence of evidence from many criteria which must be the final test in the determination of origins . . ."

A few quotations will illustrate this point. Payson (1922) says, "There is much evidence for believing that *Lesquerella* originated at some point in Central Texas and from this point as a center has spread over the large area that it now occupies . . . From purely theoretical standpoints also, the greatest number of species might be expected to occur in the vicinity of the point of origin, since there the genus would have existed for the longest period of time." In a recent publication on *Ceanothus*, Mason (1942) says, "The occurrence of many isolated local species along the coast as against a few widespread species of the interior would indicate that the direction of the *Ceanothus* migration was from the coast to the interior."

Another example of the use of this criterion, which also is admirably supported by phylogenetic and geological data, is the study of *Gaylussacia* by Camp (1941). He says, "it becomes apparent that the genus arose in South America for there, today, we find it as a series of interlocked species-groups still differentiating out of a common plexus, only three of which have given representative members to North America." The work of Szymkiewicz (1937) indicates a concentration of Mediterranean species of various genera, especially endemic species, in western Mediterranean regions. One example of this type will be sufficient. Širjaev (1934) has carefully mapped the distribution of the members of the Mediterranean genus *Ononis* and makes the following statement concerning center of origin: "Das Entstehungszentrum der Gattung (*Ononis*) war wahrscheinlich auf der Iberischen Halbinsel und im nordwestlichen. Mediterraenen Afrika, wo jetzt noch alle Subsektionen und viele endemische und fast alle älteren Arten sich konzentrieren, während im ostlichen Teile des Mediterraeneums keine eigene Subsektion und nur drei endemische Arten anzutreffen sind . . . Die Migration aus dem Entstehungszentrum fand in verschiedenen Epochen auf verschiedenen Wegen Statt." The investigations of Van Steenis (1934-1936) on isoflors (lines connecting regions of equal numbers of species in a genus) offer another method in which a strong indication of center of origin is obtained. Perhaps the most intensive studies of plants and their centers ever made are those of Vavilov (1940) and his colleagues. The following quotation is pertinent:

"Cultivated species as well as their closely allied wild relatives in their evolution, during the course of their distribution from the primary centers of species-formation, have been differentiated into definite ecological and geographical groups . . . Primary regions are at present characterized, as a rule, by the presence of many different species (in the sense of Linnaeus). They reveal practically the entire systems of genera."

It is necessary, however, to recognize that this criterion can not be accepted as universal, for it only describes a tendency that, under certain conditions, is counteracted by the operation of other factors, as is also true of age-and-area. A few of these conditions will be described.

Requirements for the development of many species are either that the forms are allopatric and have geographic isolation or, if sympatric, that they have some form of genetic (internal) reproductive isolation. Regions in which there are many closely related species are usually regions of habitat diversity, as noted by Vavilov (1940). It is entirely possible then that a phyletic stock that has had its origin elsewhere may, through migration, encounter a region in which there are numerous available ecological niches that are unsaturated—that is, in which competition pressure is low. Such a region may provide a variety of habitats with at least partial isolation. Under these conditions a phyletic stock may show a “burst” of evolutionary radiation. It is apparent that such a region of polymorphism is not necessarily indicative of the original center of origin nor of dispersal, but is a fortuitously derived secondary center of differentiation. Two more examples of this general type can be taken from Fernald’s (1926) criticism of age-and-area. He uses the conclusions of Schonland (1924) concerning *Erica*, which has nearly one thousand species in South Africa. There is not a single known fact that indicates that the genus arose in South Africa where there are the most endemics and the greatest diversity (species and sections). Furthermore, Willis had concluded that the number of endemics in any genus would rise gradually to a maximum at or near the point where the genus entered a land area, or where a genus had its center of origin. Of this corollary of age-and-area Schonland (1924) says, “Applying this prediction to the genus *Erica* in South Africa, this point would be a part of Southwest Cape Colony west of George, where not only a large number of endemics are massed, but where, moreover, the greatest diversity owing to formation of subgenera and derived genera is to be found; but I fear no contradiction when I assert that it is certainly not the place where the genus *Erica* entered South Africa, or where it originated.”

Further evidence as to the care required in arriving at conclusions concerning geographic problems is illustrated by *Senecio*. J. Small (In Willis, 1922) localizes the evolution of the Composites through *Senecio* in the northern Andes in Upper Cretaceous time, because of the present great expansion of that large genus in the Andean region. *Senecio* in the mountains of tropical America is in the most active stage of maturity, according to Greenman (1925), not because it originated there, but because it is a region geologically young and diversified. Small’s and Willis’ conclusion regarding *Senecio* rest on what Fernald (1926) gleefully calls a “colossal geological error,” because the present great elevation of the Andes, where *Senecio* now has its magnificent development, did not occur until the close of the Tertiary (Pliocene) and the beginning of the Pleistocene. From Schuchert’s (1935) recent historical geology, however, it appears that the Cordillera Occidental and the still more western and low Cordillera de Choco of northern South America are more ancient elevated land masses than

the central and eastern Andes on which pre-Cenozoic plant developments might well have occurred, and from which much of the modern Andean flora must have been derived.

Another exception to the center of origin being where the greatest differentiation of a type exists is that resulting from polyploid complexes. Polyploidy tends to break down genetic barriers between species with a resultant production of a large number of varieties and species (Stebbins, 1940). Examples of such complexes include *Crepis*, *Zauschneria*, *Rosa*, *Rubus*, and sections of *Potentilla*, *Antennaria*, and *Taraxacum*, and dysploidy may increase the intricacy of the complex. Goodspeed and Bradley (1942) note the conclusion of Kostoff (1938) that amphidiploids from F_1 hybrids may give rise to monomorphic species, but in other cases, if a series of segregated forms can survive, a polymorphic species is produced. Inconstant amphidiploidy may originate a series of adaptable forms and provide suitable material for natural selection. In every case, according to Stebbins, the majority of the basic diploids are relatively restricted in area, while most of the widespread types are polyploid. He says, "The center of distribution of the diploid species of a polyploid complex is naturally the center of variation of the complex as a whole . . . the diploids tend to occupy the older, more stable habitats. This makes the study of polyploid complexes very important from the standpoint of plant geography." Such centers of variation as are due to hybridization and polyploidy may develop at the center of origin of a genus, but that is not necessarily the case. The American species of *Crepis* have such a center in the Pacific Northwest, but the stock immigrated from the Asiatic center of the genus (Babcock and Stebbins, 1938).

A third type of exception to the criterion consists of such phylogenetic stocks as have developed a center of variation at the center of origin, in the orthodox manner, but which have suffered a decimation of the group at the center as a result of physiographic and climatic changes. Through emigration and extinction due to climatic and physiographic changes the variety of types may be reduced in one region so that a secondary center comes to contain more variety.

Hultén (1937) has also come to the conclusion that "it must . . . be unsafe to assume that a plant originates in the place where it has its most numerous relatives. In most cases such a consideration will perhaps be correct, but in others it must be misleading." He illustrates this point by reference to old, widespread, arctic-montane species. "It is natural therefore that in different parts of the area of a Linnaean species considerably differentiated races should be found. The area has repeatedly been split up, during the glacials under the influence of a cold climate in the north and a pluvial one in the south, and during the interglacials under the influence of drought and heat. Each of these agencies must have caused a selection of biotypes in its particular direction . . .

The idea is current that a district in which a plant shows much variation or has many closely related species must be its original home. According to the above point of view this would only mean that the plant has been present within the district for a comparatively long time and has developed in different directions under the pressure of varying conditions there . . . The similarity or dissimilarity of two types alone will hardly be able to settle discussions concerning relationship between them." This latter conclusion is arrived at by Hultén because of the complication resulting from "parallel selection" of biotypes by separated but climatically similar regions.

We have seen that the location of greatest differentiation of a type may be at the center of origin of the group and, also, that the criterion can not be uncritically applied for a number of reasons.

CRITERION 2. LOCATION OF DOMINANCE OR GREATEST ABUNDANCE OF INDIVIDUALS

In connection with this criterion it first is necessary to note that dominance is a matter of the control of a community through reaction and coaction, and abundance is only a matter of numbers of individuals. It is true that certain forms may exert dominance through mere numbers, and that is possibly more frequent among plants than animals, but often it is true that less abundant forms are dominants by virtue of their life-form or strong actions.

Species that are dominants in a certain community (and there are usually not very many such species relative to the floristic composition of the community as a whole) usually range more widely than the area of the community. For example, beech, sugar maple, hemlock, and yellow birch all range more widely than the northern hardwood climax association in which they are co-dominants. It seems to me that dominance for a species can have no meaning except in terms of community dynamics. If, however, we consider a genus, there may be some instances in which the regions where certain species are community dominants or codominants are also the regions where there is a large concentration of species of the genus. This appears to be true for *Quercus* and *Hicoria* in the Ozark and Cumberland regions. Even here, however, a different interpretation is likely. These are ancient land areas in which evolution has long been going on and the numbers of species and their dominance may be unrelated phenomena, and also unrelated to center of origin.

The center of greatest abundance of individuals, center of frequency, has a special meaning only in connection with the distribution of the members of a population, a subspecies, a species, etc. The assumption that the center of abundance is also the center of origin for the type has to be based, it seems to me, on an hypothesis that the species arose in the habitat where it is best capable of abundant reproduction and establishment. This is a gratuitous assumption.

It is reasonable that, with migration from the center of origin, a species population may encounter more favorable conditions than those that prevailed where it arose. Hultén (1937) says concerning the "mass center" hypothesis, "Christ and other authors considered that a plant is likely to have originated in a district where its most numerous individuals are now found. Heer already opposed this view. It is natural that if a plant at the border of its perhaps wide original area should find favourable conditions and multiply freely, so that numerous individuals are developed, such a phenomenon will afford no indication of the earlier history of the species." Such cases are apparently found in certain weedy species of *Tradescantia* that have obtained wide areas and relatively high abundance in the eastern grassland and agricultural areas (Anderson and Woodson, 1935). Also, as with criterion 1, we can conceive of climatic deterioration causing a reduction in numbers of individuals at the center of origin.

Shreve (1937) has pointed out that shrubs of the Sonoran desert with hard wood, sparse branching, and determinate growth (*Cassia*, *Mimosa*, *Acacia*, *Croton*, *Karwinskia*, *Caesalpinia*, *Lysiloma*, *Bauhinia*, *Acalypha*, etc.) belong to genera which are well represented in the thorn-forest, both with respect to numbers of species and abundance of individuals. Furthermore, distributional data indicate that this type has spread from the thorn-forest into the desert. However, Shreve (1934) has clearly shown for *Larrea tridentata* and *Franseria dumosa* what is probably a widespread relationship—that variations in plant size and abundance, and degree of dominance are correlated with environmental conditions, and not with the center of origin.

It is of interest to inquire further into certain characteristics of the distribution of individual plants. Gleason (1925) has studied this matter statistically and concluded that environmental differences are not of sufficient magnitude to affect the distribution of the species within an association, and that the number of individuals of a species, other things being equal, is an index to its adaptation to the environment. But what, we may ask, is the behavior of the species outside its native association, or at the margin of its range? When the area of a population of a new species or subspecies is expanding from its center of origin, and when natural barriers have not yet established a boundary, there will naturally be a centrifugal decrease of density. This would seem to be an inevitable result of numbers and random dispersal, and to provide a case in which the criterion is true. Let us assume, however, that a species population has extended its area to its maximum, having met barriers of one sort or another on all sides. Under these conditions it would seem that there would be a tendency for a greater density of individuals to exist toward the center of area because of a central harmony between ecological requirements and ecological conditions. Everywhere outside of this central "typical" climatic region

to which the species is adapted there will be, for it, a progressive deterioration of the climatic type. That is, in marginal regions of the climatic type where it begins to grade into another climatic type, there will be fewer and fewer suitable spots for the species. Of necessity, if this picture be true, the density of the species will tend to decrease toward the periphery. Some interesting data concerning the behavior of species at the margin of range have been published by Griggs (1914) on the Sugar Grove district of southern Ohio. He says, "It is clear . . . that in this region the species in which the individuals become scarcer and scarcer until it fails altogether is exceptional." Certain species are approximately continuous up to the margins of their range, but others are increasingly discontinuous until they are characteristically disjunct, and sometimes widely so, in the peripheral portion of their areas.

In the light of these data, it would seem that the criterion of species dominance and density is by no means an infallible guide to center of origin. Dominance and density are frequently highly irrelevant in this respect.

CRITERION 3. LOCATION OF SYNTHETIC OR CLOSELY RELATED FORMS

From the context and through correspondence I find that by "synthetic" is meant generalized or primitive forms of a phyletic group. With this half of the criterion we can have no quarrel this far: the most primitive form or forms of a group certainly arose somewhere, and wherever that was, there is the center of origin of the group. To ascertain that center, after a group has had a long history, is, however, another matter.

It is frequently claimed that the center of origin for a group is where the earliest fossil forms have been found, whether or not the group is represented there today. For example, it has been claimed that the shell family Pleuroceridae had a western origin because its earliest record is from the Laramie formation (Colorado, etc.). Adams (1915), however, concluded that the family, and especially *Io*, had a southeastern origin centering in eastern Tennessee despite the absence of substantiating fossils.

There are two diametrically opposed views. The most widely accepted view is that the most primitive members of a group are still to be found at or near the center of origin of the group. This is frequently true because most of our temperate genera date back to the Cretaceous or early Tertiary and their primitive forms are frequently found concentrated in the old land areas. In the United States, for example, such ancient land masses with primitive species (Gleason, 1923) include the Southern Appalachian center, the Cumberland and Ozark center, the prairie center of Nebraska, Kansas, and eastern Colorado, the southwestern desert center, etc. In a study of *Lesquerella*, Payson (1922) concluded that the center of origin of the genus was in the old land area of central Texas where "not only are these species primitive, but in no

other locality may be found anything like an equal display of what have been considered ancestral characteristics for purely morphological reasons . . . The periphery in general is bounded by highly specialized members of the genus."

The opposite view concerning the location of primitive species of a group is that the primitive forms are to be found at the periphery of area because they have been crowded from the center by the younger and more aggressive members of the group. The employment of such a criterion as this depends in part upon the validity of taxonomic criteria for the indication of primitiveness. Many of these criteria (as enunciated for botanists by Bessey, and others) themselves deserve critical analysis.

One of the most skillful proponents of the view that primitive forms are peripheral is Matthew (1939). The following quotations from "Climate and Evolution" (pp. 10, 11, 31, 32) reveal his hypothesis which is extensively documented by vertebrate paleontology and phylogenetics, but not universally accepted.

"Whatever agencies may be assigned as the cause of evolution of a race, it should be at first most progressive at its point of original dispersal, and it will continue this progress at that point in response to whatever stimulus originally caused it and spread out in successive waves of migration, each wave a stage higher than the previous one. At any one time, therefore, the most advanced stages should be nearest the center of dispersal (original), the most conservative stages farthest from it . . . to assume that the present habitat of the most generalized members of a group, or the region where it is now most abundant, is the center from which its migrations took place in former times appears to me wholly illogical and, if applied to the higher animals as it has been to fishes and invertebrates, it would lead to results absolutely at variance with the known facts of the geological record . . . The successive steps in the progress must appear first in some comparatively limited region, and from that region the new forms must spread out, displacing the old and driving them before them into more distant regions. Whatever be the causes of evolution, we must expect them to act with maximum force in some one region; and so long as the evolution is progressing steadily in one direction, we should expect them to continue to act with maximum force in that region. This point will be the center of dispersal of the race. At any period, the most advanced and progressive species of the race will be those inhabiting that region; the most primitive and unprogressive species will be those remote from this center."

Cytogenetics is providing a body of information for several groups that points undeniably toward the forms that are primitive in a group. One example of this type will be sufficient. Anderson (1937) says, "In those species which have both diploid and tetraploid races we . . . know that the tetraploids must have originated from the diploids." Tetraploid *Tradescantia occidentalis* ranges throughout the Great Plains and the eastern Rocky Mountains, and has a small diploid area in central and eastern Texas. Tetraploid *T. canaliculata* occupies a wide area in the Mississippi Valley, and is diploid in the same territory in

Texas. Also, *T. hirsutiflora* and *T. ozarkana* exhibit the same tendency. The combination of cytology with geological history and taxonomy suggests very strongly that the Edwards Plateau area of central Texas was the immediate center from which the American *tradesantias* have developed in comparatively recent times.

With respect to the other point of the criterion, it can be said that closely related forms can come to be located almost anywhere within the generic area. The nearest relative of any form, however, will tend to be near by, at least at first, because of the filial relationship between them. According to Kinsey (1936), the picture of evolution is that of a simple or infrequently branching chain. In this chain each species is a derivative of a previously existing species, usually without extermination of the parental species.

When one looks at a large family of plants, it is apparent that it is not everywhere equally well developed or rich. A certain tribe composing, say, 10 per cent of the family, may in one region constitute 30 or 40 per cent or more of the family. This phenomenon is likely true for the other tribes. Such regions of differentiation are likely regions of speciation or origin, except where, for historical reasons, they are known to be regions of preservation. I can not see, however, that closeness of relationship among species can ever be employed as a criterion to indicate the geographic center of origin of a group without the aid of other facts. We can only say that primitive and closely related forms may or may not be at the center of origin.

CRITERION 4. LOCATION OF MAXIMUM SIZE OF INDIVIDUALS

In a discussion of evolution of species through climatic conditions, Allen (1905) reiterates some "laws" stated by him in 1882: (1) the maximum physical development of the individual is attained where the conditions of environment are most favorable to the life of the species; (2) the largest species of a group (genus, sub-family, or family) are found where the group to which they severally belong reaches its highest development, or where it has what may be termed its center of distribution.

These conclusions were reached from the observation that "in the northern hemisphere, in nearly all types of both birds and mammals of obviously northern origin, there is a gradual decrease in the general size from the north southward in the representatives of a conspecific group . . ." Later on he says, "The variation in size from north southward is as gradual and continuous as the transition in climatic conditions."

It seems to me that within these statements, employed by Adams and others, the "cat is out of the bag." In the first place, size is a specific character that may not be related to environment. Size differences may be due to biotype selection across a climatic gradient, or to phenotypic expression. Allen's state-

ments concerning size and favorableness of environment are generally correct, but there is no necessary relationship between size and center of origin or center of distribution. It would seem that geographic trends in adaptive characters are usually nothing more than the *clines* of Huxley (1940). Allen's statements were questioned by Cockerell (1906) who said, "I found in that genus (*Hymenoxys chrysanthemoides*) a case which seemed to me to exactly agree with those postulated by Dr. Allen, except that the large form was southern, the small one northern." To take another case, it is a common observation among botanists that plants on oceanic islands, such as the Azores, Canaries, and the Galapagos, are frequently of larger stature than their relatives on the mainlands from which they were derived. This larger size of herbs, shrubs, and trees would seem to be related to the long growing season, rather than to any hypothetical indication of their island origin.

I have tried to find an authentic case among plants either in favor of the criterion or opposed to it in which the data are adequate, but have failed to do so. The following notes are only suggestive. *Prosopis*, for example, attains its largest size (height of about 50 ft.) in the Rio Grande valley, where the genus is near its periphery. Shreve (1936) says, "It is only in the most favorable situations that the mesquite is found as a tree. In less favorable ones it is merely a shrub." The genus, however, is taxonomically complicated (Benson, 1941) and has had a long and obscure history as indicated by its split range, being in the South American deserts as well as in Mexico and our Southwest. It is therefore impossible to be very certain concerning the history of its area. The Southern Appalachians are becoming famous for their large trees as the region is better known. The largest single specimens known of *Picea rubens*, *Tsuga canadensis*, *Aesculus octandra*, *Tulipastrum acuminatum*, and several others, are found localized in the Great Smoky Mountains, but there is no evidence to indicate the origin of these species in that region.

One situation in which the tendency is opposite to the criterion has been shown by cytology. Autotetraploids, and sometimes allotetraploids, are larger than their progenitor diploids. Furthermore, they have a strong tendency to extend the range of the group and to occupy peripheral positions relative to the diploids. (Anderson and Sax, 1936; Babcock and Stebbins, 1938.)

CRITERION 5. LOCATION OF GREATEST PRODUCTIVENESS AND ITS RELATIVE STABILITY IN CROPS

From Adams' comments, it appears that he considers productiveness to be closely related to size and numbers, and essentially a matter of growth and reproduction. According to Adams, Hyde (1898) concluded that crop production, whether it averages high or low, will tend to be more uniform from year

to year in the region where the crop is indigenous, and that the variability from year to year increases with departure from that center.² In the first place, note that Hyde indicates that the crop production is not necessarily high at the region of center, or where the crop is indigenous, but only that it is uniform from year to year. This does not fit well with criteria two and four. Furthermore, it does not appear that the term "indigenous" is employed in its strict meaning of being "native," but in a more general meaning of being "at home" in the sense of being well adapted. It is, of course, well known that crop production shows the greatest stability from year to year in climatic areas to which it is best adapted. This phenomenon appears to have nothing to do with center of origin of the crop (Vavilov, 1928, 1940), but is explained by weather and the operation of limiting factors (Taylor, 1934).

CRITERION 6. CONTINUITY AND CONVERGENCE OF LINES OF DISPERSAL

When the species of a genus or higher category are distributed along natural highways of migration, and when these highways converge on a certain area, the distributional pattern suggests that the region of convergence of these routes is the center of origin and dispersal. This suggestion is even stronger when, as is usually the case, unrelated organisms show the same pattern. There is, however, no *a priori* reason considering dispersal lines alone why migrations need have been divergent from the apparent center rather than convergent on it. It is usually not difficult, however, to obtain evidence (see criterion eight) as to which direction the migrations took. Such evidence is largely obtained from comparative morphology and relationships. Sometimes paleontological evidence helps indicate the direction of migration. In other cases cytogenetical analysis of the related forms reveals without doubt the direction which the movement has taken. Migratory tracts are merely lines (however broad) of frequent, suitable habitats, and are not necessarily one-way routes. As expressed, and by itself, the criterion is not valid.

CRITERION 7. LOCATION OF LEAST DEPENDENCE UPON A RESTRICTED HABITAT

The use of this criterion for the indication of center of origin depends upon a species being more polymorphic at the center of origin (Criterion 1) or upon more primitive forms having wider tolerances than derived forms. Both of these conditions may not be true. A wide species contains a very large number of biotypes, perhaps many thousands (Turesson, 1925, 1932; DuRietz, 1930). Progressively from the center of origin, and especially along narrow migratory tracts extending from the main area, there is a biotype depauperization. This can result from partial isolation due to distance alone. A remote portion of a population does not in practice, even if in theory, have access to the entire

²Recent investigations are summarized by Klages (1942).

stock of genes of the species as a whole. When a species is divided into geographic subspecies and ecotypes, these conditions probably apply to them also, but less obviously. No species is completely panmictic.

On a basis of the Law of Tolerance (Good, 1931), it is concluded that each individual organism can live only within the inherent limits of its tolerances for the environment, and the tolerances of a species is the sum of the tolerances of the component individuals of the species population. Now it seems to me that this summation of Good's can have no real meaning for an individual. No individual can contain (inherit) all the genic variability of the population, although in a panmictic population any individual might theoretically contain any possible pair of allelomorphous genes. In many cases it is an observed fact that morphological polymorphism decreases away from the center of area of a species or subspecies. Although it is more difficult to demonstrate, it is reasonable to assume that individual members of a species differ as much physiologically as they do morphologically. In fact, it seems entirely likely that adaptation and ecological amplitude reside more in unseen features than in the characters of the type usually employed in systematic studies. Both, of course, ultimately result from the genic constitution of the individuals, and may be linked. In this connection Hiesey, Clausen and Keck (1942) say, "Within populations, hereditary variants occur, some of which may possess physiological qualities that give them the potential capacity to survive in different kinds of places. Other variations seem to have no significance for survival, representing random differences that are not incompatible with the main requirements of existence in their population." Just as individuals vary within a population, so may populations show a statistical difference, which may or may not be adaptive and favor survival. It would seem to follow, then, that when polymorphism is greater near the center of area than at its periphery, it is entirely likely that there will be less dependence upon a restricted habitat at the center of area. This should not lead to the assumption that any one individual has a wider tolerance and a lesser dependence upon a restricted habitat because it happens to live near the center of area.

If primitive members of a group have a wider tolerance than more advanced ones, and if primitive members are more likely to be found near the center of origin, there should be a lesser dependence upon a restricted habitat at the center. The wide ecological tolerance that primitive species are supposed to have is sometimes based on the paleontological evidence of large areas which species of modern genera are known to have had in Cretaceous or Tertiary times. This is frequently a spurious argument because many of these species are known not to have had these wide areas synchronously, and furthermore, little is known of ecological subdivisions of the species. Finally, there are no physiological studies, so far as I know, which indicate that primitive species

have unusually broad tolerances. Circumstantial evidence, on the contrary, indicates that old relic species are frequently markedly restricted in area and habitat type.

This problem has received at least one excellent consideration in paleobotanical literature. After pointing out that certain fossil floras of later Tertiary age contain mixtures of plants from widely different habitats, Axelrod (1941) suggests that the explanation may not be due only to overlap of floras (in ecotonal regions, or from migratory mingling), or to the fact that Miocene and Pliocene vegetation was "generalized" and modern forests derived by "climatic segregation only in the late Cenozoic," but to the ancient existence of ecospecies. For example, *Sequoia Langsdorffii* (close to *S. sempervirens*) was variously associated with species of boreal, warm-temperate, and temperate type. Other modern endemics, now of restricted type, but of once wider association, include *Lyonothamnus*, *Ginkgo*, *Glyptostrobus pensilis*, *Picea Brewsteriana*, and *Quercus tomentosa*, according to Axelrod. He says, "it seems highly probable that many Miocene and Pliocene species related to living endemics may represent extinct ecotypes of more widely distributed Tertiary ecospecies." Probable as this concept is, it still does not show that primitive species are of wide ecological tolerance and recent ones of narrow amplitude. The late Cenozoic was a time of climatic breakup and, for many species, biotype depauperization with only "senile," relic endemics remaining; but, as Axelrod supposes, the wide area and diversified conditions under which certain Tertiary species lived were due to the biotype (ecotype) richness of the species as a whole. That richness represents the mature condition of a species history. As with previous criteria, we find ourselves confronted by many "ifs." The above arguments concerning the region of least dependence upon a restricted habitat are applicable in the determination of center of origin only when the center of origin is also the center of variability, and when the center of origin has not been disturbed and reduced in biotype richness.

The idea that a species is usually ubiquitous in the center of its range, occurring in all kinds of places, and restricted to only the most favorable sites at its areal limits, according to Griggs (1914), is probably attributable to Blytt, and has been favored by Cowles. This idea includes the assumption that the favorable climate in the central portion of the species range somehow overcomes diverse edaphic factors, whereas at the margin of range edaphic factors permit a spotty extension of area. I remember Cowles, when lecturing on the dunes of Lake Michigan's shores, saying of the cactus, "It sits on the southern and western slopes, looking toward its home." There is, of course, a large element of truth in this generalization, as is shown by the usual disposition of preclimax and post-climax communities in any region.

Let us turn again to the often cited polyploids. Anderson (1937) says, "The diploid species are of limited distribution and even in those areas where they do occur are usually restricted to one particular habitat. By contrast, the tetraploid species and races have wide distributions and most of them have the ability to flourish under a variety of situations." Allopolyploids, especially, may combine the tolerances of their diploid progenitors.

In amplifying his discussion of this criterion, Adams (1909) selects what seems to me to be a particularly vulnerable example. He says, "Outlying colonies tend to have a limited or restricted range. At the same time such colonies are peculiarly liable to become extinct, as they are usually near the limit of favorable conditions . . . this is true of the 'boreal islands' in swamps within the glaciated portion of the continent. For example, members of the tamarack bog association, toward their southern limit, have very restricted or local range; but to the north, *the bog forest conditions, as it were, spread from the bogs proper and become of extensive geographic range*, as the water beetles invade the damp mosses . . . These restricted, attenuated, or isolated colonies, dependent upon special conditions, are clearly indicative that they are pioneers or relics, which point toward the region where the range is spread out and becomes of geographic extent." I have italicized a portion of the above quotation to emphasize the fact that the areal pattern is apparently wholly dependent upon the pattern of occurrence of suitable conditions. This is an ecological matter that of itself denotes nothing concerning origin. Adams goes on to say that the isolated colonies are *either* pioneer or relic, destroying his own thesis, it seems to me.

CRITERION 8. CONTINUITY AND DIRECTNESS OF INDIVIDUAL VARIATIONS OR MODIFICATIONS RADIATING FROM THE CENTER OF ORIGIN ALONG HIGHWAYS OF DISPERSAL

This criterion, related to number six, frequently is a reliable one. With respect to changes in character frequency (as shown by the mass-collection techniques: Fassett, 1941) we can only conclude that there can be a gene flow in any direction through a population. Any attenuation of the frequency of a certain gene is presumably direct evidence of the center of origin of that gene in the region of highest frequency. One of the most interesting cases of this sort concerns the distribution of the recessive melanistic mutation in *Cricetus cricetus*, the hamster. Timofeeff-Ressovsky (1940) says, "In the course of the last 150 years this mutation has spread from its original center of high concentration along the northern border of the species-area . . . populations with rather high concentration of this gene are spread westward as far as the river Dnieper." Apparently the melanistic form is adaptive in the wood-steppe ecotone along the northern portion of the species area, and this is one of the few

cases in which it is definitely shown that mutations participate in the origination of geographical races.

When introgressive hybridization (Anderson and Hubricht, 1938) is demonstrable and when a series of chromosome changes, such as a polyploid series, can be shown along highways radiating from a center, it would seem that the indication of center of origin is incontrovertible. When several characters show a parallel and direct continuity of gradation of frequency or of modification, it is likely that there has been active migration of the population from a center. This is sometimes recognizable by chains of subspecies, pairs of species, etc. Payson's (1922) work on *Lesquerella* provides a good example based on comparative morphology. He says, "In a graphic representation of the subsectional groups they may be shown by lines radiating from a common center. Such a diagram could be superimposed upon a map and in nearly every case the species at the base of each line of development would be nearer the Texas region (center of origin) than species derived from it."

Once again it can be said that this criterion alone is of no significance. A geographic series of size expressions may be due to environmental conditions reflected in growth responses (phenotypic changes in a genotype) or it may be due to selection operating through a region of gradually changing environment. When morphological, phylogenetic, and geographical data are used to support one another, the validity of the conclusions regarding direction of migration depends upon the validity of the morphological criteria employed.

CRITERION 9. DIRECTION INDICATED BY GEOGRAPHICAL AFFINITIES

This criterion is frequently valid for organisms located at stations removed from the major area they occupy. As mentioned earlier, in any region there are usually numerous extraneous species representing two or more different floristic elements, and recording as many different migrations in the vegetational history of the region. In this connection Grinnell and Swarth (1913) say, "We cannot expect to derive universal laws for the behavior of species, to be applicable uniformly in any region . . . where two faunas meet . . . Upon reflection it is difficult to conceive of precisely the same set of delimiting factors operating upon any two species alike." For extraneous species, it is frequently a fairly safe assumption that they were derived from the areas where they have their principal distribution. If a genus or family is largely characteristic of a single formation or climatic type, and has one or a few species of different type, it is likely that the latter migrated and evolved from the generic center. Bromeliads have migrated away from the humid tropics and entered the deserts of southern Mexico, and, conversely, cacti have migrated out of the desert region and established themselves as epiphytes in the tropical forest, according to Gleason (1923). No one suspects certain rather large tropical groups as hav-

ing a temperate origin because of a few temperate representatives, as in *Diospyros*, *Tripsacum*, and *Phoradendron*, but quite the contrary. The point is well illustrated by a quotation of Merrill (1936). "When a genus is described from material collected in a certain place and is known only from that region for many years, we more or less automatically accept it as a group characteristic of that region. If a representative of it is later found in another area, we are apt to consider it as an extraneous entity there."

Returning to our own region we can cite an example. Typical Atlantic and Gulf coastal plain species have long been known from the Appalachian and Cumberland uplands (Gattinger, 1901; Kearney, 1900). Sometimes these inland plants are rare, and stations are of small area and widely disjunct from the coastal plain where the species are now common. Fernald (1931) has correctly hypothesized the origin of some of these species on the old lands that are now part of the Cumberland plateau, and Braun (1937a, 1937b) has found them most abundantly in the undissected portions of the now elevated peneplain. Fernald says, "With the Tertiary uplift of the Appalachian region and its final conversion into a vast well-drained mesophytic area . . . the Cretaceous xerophytes and hydrophytes which had previously occupied the ground gradually moved out to the newly available and for them more congenial Coastal Plain and similar habitats to the west and northwest." In such a case as this, the principal area is a derived one and is no indication of the center of origin. It really is not a question of coastal plain plants in the Appalachian and Cumberland uplands, but of upland plants in the coastal plain, if we view the relationship historically. Not all coastal plain species in the interior have had this history. In his monographic study of the Scrophulariaceae, Pennell (1935) has detected some forms that have migrated from the coastal plain into the Piedmont and the Blue Ridge provinces.

The direction of dispersal and the center of origin are many times indicated by geographical affinities, but the criterion can not be used alone, and the principal area and biographic type may be derived and the minor area relic.

CRITERION 10. DIRECTION INDICATED BY THE ANNUAL MIGRATION ROUTES, IN BIRDS

Applied to plants, this criterion would be restricted to species whose diaspores are bird disseminated, either epizooically or endozooically. If the migration takes place both northward and southward over the same route, as for some species employing the Mississippi valley and others using the Appalachian uplands, direction of plant movement is not necessarily indicated. In cases where the northward and southward migration paths are not coincident, the direction of movement is indicated.

CRITERION 11. DIRECTION INDICATED BY SEASONAL APPEARANCE

Although Adams was aware of this criterion at the time of publication of his first list (1902a), he did not include it until later (1909). In the northern hemisphere, vernal activity suggests boreal origin. He also thought that there is an altitudinal as well as latitudinal relationship, i.e., that mountain forms spreading downward should belong to the vernal aspect, and lowland forms spreading upward should belong to the aestival aspect.

It is undoubtedly true that such relationships between origin and aspect occur. It does not seem to me, however, that this criterion expresses any inherent indication of origin. The described relationship could exist, for example, for a form or series of forms occupying montane, subalpine, and alpine belts (or the corresponding latitudinal zones) with the center of origin in either terminal belt or the middle. The limitations to the spread of a form are found in the action of the whole environment upon the physiology of the form, with such factors as temperature, light intensity, and photoperiod operating. Therefore, it would seem as easy and sound to conceive of a vernal form of the south spreading northward with a change to aestival aspect, as the reverse. This fact seems to me to illustrate perfectly the pitfalls of deductive reasoning and generalization.

CRITERION 12. THERE IS AN INCREASE OF THE NUMBER OF DOMINANT GENES
TOWARDS THE CENTERS OF ORIGIN

This criterion could only have been proposed after the development of genetics and is appended to the older ones of Adams because of its apparent validity. It can, I think, be attributed solely to Vavilov (1927), who said, "The direct study of the centres of the origin of cultivated plants . . . has revealed not only a great diversity of forms but also a prevailing accumulation of dominant forms characterized by dominant genes in the centres. A considerable number of plants investigated show this regularity . . . The secondary centres of the origin of forms are, on the contrary, characterized by a diversity of chiefly recessive characters."

Several cases are discussed by Vavilov, but only one will be mentioned here by way of illustration. The center of origin of cultivated rye and the genus *Secale* to which it belongs is in Eastern Asia Minor and Transcaucasia. Here are all the species of rye and the whole diversity of characters of the varieties; but also here are concentrated the dominant characters of red-eared, brown-eared, black-eared, and marked pubescence of flowering glumes. In the secondary centers are such recessive characters as liguleless leaves, yellow-ears, and glabrous glumes. Cultivated plant types in their progress from their principal genetical centers seem to exhibit a "falling out" of the dominant genes and

"proportionally to the spread of isolation, proceeds the accumulation of recessive forms."

CRITERION 13. CENTER INDICATED BY THE CONCENTRICITY OF PROGRESSIVE EQUIFORMAL AREAS

This criterion, developed by Hultén (1937), primarily concerns centers of dispersal for arctic and boreal biota from refugia; but it also concerns centers of origin when evolution as well as migration has occurred. Hultén's thesis is as follows: from a refugium, each species tends to spread in all available directions, but because of different tolerances and capacities for dissemination it could not be expected that all plants would spread to the same extent or with the same rapidity. The result is a tendency toward the development of approximately circular areas of different size around the center; but in nature the theoretically circular form of areas is seldom attained because of various barriers. There still remains, however, the chief feature of areas: those plants that radiate from the same center have progressive equiformal areas of different size. This criterion is obviously related to number six stated by Adams. As developed by Hultén, however, there is a clean-cut scientific basis with the conclusion reached through strictly inductive reasoning.

CONCLUSION

There seems to be only one conclusion possible, and it carries implications far beyond the scope of the present discussion of criteria of center of origin. The sciences of geobotany (plant geography, plant ecology, plant sociology) and geozoology carry a heavy burden of hypothesis and assumption which has resulted from an over-employment of deductive reasoning. What is most needed in these fields is a complete return to inductive reasoning (Raup, 1942) with assumptions reduced to a minimum and hypotheses based upon demonstrable facts and proposed only when necessary (Hultén, 1937). In many instances the assumptions arising from deductive reasoning have so thoroughly permeated the science of geography and have so long been a part of its warp and woof that students of the field can only with difficulty distinguish fact from fiction.

THE UNIVERSITY OF TENNESSEE
KNOXVILLE, TENNESSEE

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